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BODY FLUID COMPOSITION AND AERIAL OXYGEN CONSUMPTION IN THE FRESHWATER MUSSEL, *LIGUMIA SUBROSTRATA* (SAY): EFFECTS OF DEHYDRATION AND ANOXIC STRESS

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A number of bivalve molluscs are intermittently exposed to air (Bayne, 1973; Kuenzler, 1961; Lent, 1968; Moon and Pritchard, 1970). Usually the valves are closed and it is generally accepted that the animals are under anaerobic conditions (Dugal, 1939; Prosser, 1973). However, some intertidal mussels have been observed to partially gape and consume oxygen from the atmosphere (Coleman, 1973; Kuenzler, 1961; Lent, 1968; Boyden, 1972).

The freshwater mussel, *Ligumia subrostrata*, lives in still water within 50 centimeters of the surface (Murray and Leonard, 1962). These animals will migrate with changes in the water surface level. Occasionally, receding flood waters or drying of the pond leave *L. subrostrata* exposed to the atmosphere. During this time the valves are closed and some animals will survive for several weeks. Other bivalves have survived emersion over 12 months (Dance, 1958).

Epithelial tissues used in gas exchange are permeable to water. When exposed to an atmosphere with high relative humidity, water loss is minimal. However, prolonged exposure to a low relative humidity atmosphere results in significant water loss and concomitant changes in body fluid solute concentrations (Hiscock, 1953).

This report examines the roles of aerial respiration, desiccation and anoxia on changes in body fluid composition and survival of *L. subrostrata* when removed from water. Evidence is presented indicating these animals are not anoxic when out of water but maintain aerobic metabolism. However, they can tolerate forced anoxia.

Methods

Specimens of *Ligumia subrostrata* were obtained from a pond near Baton Rouge during July 1973 to March 1974. The animal shells were washed with tap water and most were used within one week of collection. Animals kept out of water were maintained at room temperature (22–25° C). Animals not immediately used were stored in tap water (3 mM $NaHCO_3$, 0.1 mM NaCl) or in artificial pond water (Prosser, 1973) at room temperature.

The valves were separated by mechanical force and mantle cavity water drained. The posterior mantle tissue was separated from the shell at the pallial line and reflected anteriorly. The body fluid which accumulates in the exposed pallial space was withdrawn by a pipet. Frequently, the posterior adductor muscle was cut to facilitate fluid collection. The fluid was centrifuged ($8000 \times g$) to

remove cells and total solute determined immediately. The remaining fluid was either diluted for other analyses or stored frozen (−20° C).

Fluid analyses

Total solute was determined on undiluted samples of body fluid using a Precision Systems Osmette (0.2 ml) or a Hewlett-Packard vapor pressure osmometer (25 μl). Sodium and potassium were determined on diluted samples using a Coleman flame photometer. Chloride was estimated with a Buchler-Cotlove titrator. Body fluid was diluted with LaO_3-HCl and calcium determined by atomic absorption (Perkin-Elmer).

Lactate and ninhydrin positive substances (NPS) were determined on supernatant of body fluid precipitated with equal volumes of cold 10% trichloroacetic acid and centrifuged at 8000 × *g*. Lactate was estimated by the Ström (1949) modified colorimetric method. NPS was measured by a colorimetric method (Rosen, 1957).

Ammonium excreted by *L. subrostrata* to the bathing medium was measured by direct nesslerization. Equal volumes of bath samples and 10% Nessler's reagent were mixed and nitrogen content determined by colorimetry. Rates of ammonium excretion were estimated from the appearance of nitrogen in the bath.

Tissue glycogen and analyses

Total body weight was determined by weighing the animals after draining the water from the mantle cavity. The soft tissue was dissected from the shell and both shell and tissue were dried to constant weight at 85° C. Shell weight was unchanged when dried further to 105° C, whereas tissue declined by 3.3 ± 0.2% (10).

Total tissue carbohydrates (glycogen) was determined by a phenol-sulfuric acid colorimetric method (Montgomery, 1957). The soft tissue of the mussel was dried to constant weight (85° C) and digested with 20% KOH (100° C). Diluted alkaline digest was analyzed directly for carbohydrate. The alcoholic precipitation of glycogen was eliminated since direct analysis agreed with precipitate analysis (± 4%).

Oxygen consumption

Aerial respiration was determined using a Gilson respirometer. Animals were transferred to 100 ml flasks (Aminco) containing 200 μl water, to maintain water saturated air, and 200 μl 20% KOH as CO_2 absorbant. Oxygen consumption was measured at 22° C for 1.5–3 hr after > 30 min equilibration period. The correction factor for O_2 consumption (Q_{O_2}) was $(P_b \times 273)/(760 \times T)$, where P_b is atmospheric pressure and T is absolute temperature under experimental conditions. All Q_{O_2} values are expressed as μl O_2/g dry tissue-hr at standard temperature-pressure. Sex and season may affect Q_{O_2} (Newell, 1970) but the data are incomplete to attempt corrections.

Oxygen consumption was determined by a modified Winkler method (Strick-

land and Parsons, 1972). Animals were transferred to containers filled with O_2 saturated pond water and sealed for 1–2 hr at 21° C. At specific times, the containers were opened and water carefully siphoned into 300 ml BOD bottles, with 150 ml overflow, for oxygen determination. The decrease in O_2 content from the O_2 measured initially in the water was used to estimate $\dot{Q}_{O_2}$.

Anoxia

Animals were transferred to pond water in a desiccator jar and tubing from a N_2 cylinder connected to an air stone in the water. The nitrogen was continuously flushed through the system and vented to the atmosphere. The pond water was changed daily with pregassed water (<54 μl O_2/l). Animals maintained in a N_2 atmosphere were sealed in a similar container but were supported out of water. The atmosphere was replaced twice each day (5 min flushing with N_2). CO_2 absorbant was also placed in the container.

Data are expressed as the mean ± one standard error. Differences between means were analyzed by the student "t" test and considered significant if $P < 0.05$. Regression lines were estimated by the method of least squares.

Results

Freshwater acclimated animals

Ligumia subrostrata body fluid concentration is among the lowest concentration found in fresh water animals. Tissue and body fluid composition for tap water acclimated mussels is indicated in Table I. Total tissue water has not been partitioned into intra- and extra-cellular compartments. The measured ions account for 72% of the total solute. Bicarbonate is probably a major anion in the body fluid which was not measured (see Potts, 1954).

Table I

Tissue and body fluid composition of tap water acclimated L. subrostrata.

Component	Units	Number of animals	Mean ± SEM
Total weight	g	26	23.7 ± 2.4
Shell	g/10g total	26	4.33 ± 0.10
Fresh tissue	g/10g total	26	5.67 ± 0.10
Mantle cavity water	g/10g total	10	1.2 ± 0.1
Tissue water	g/10g fresh tissue	18	8.8 ± 0.0
Body fluid:			
Total solute	mOsmoles/l	26	53.0 ± 0.6
Na	mM/l	26	21.0 ± 0.6
Ca	mM/l	8	4.8 ± 0.2
K	mM/l	10	0.4 ± 0.0
Cl	mM/l	26	12.0 ± 0.6
Lactate	mM/l	15	0.14 ± 0.01
NPS*	mM/l	20	1.28 ± 0.17

* Ninhydrin positive substance.

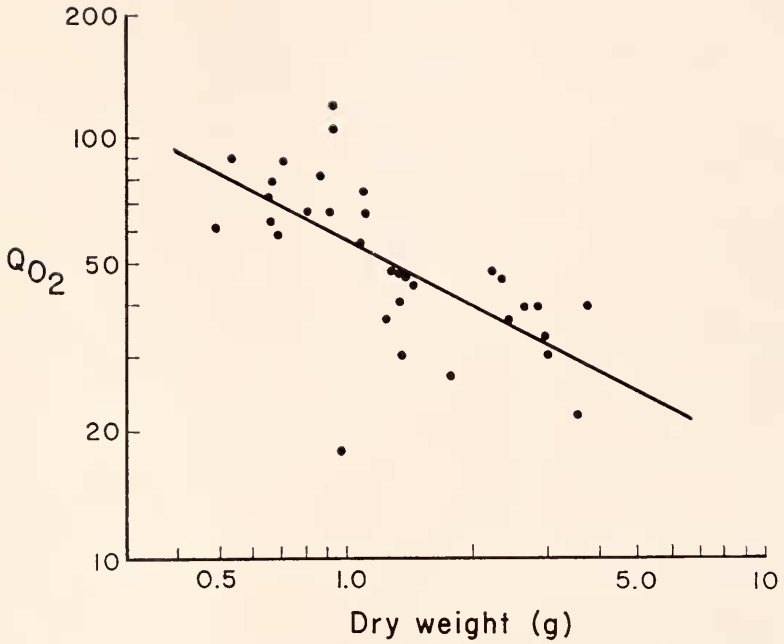

FIGURE 1. Aerial oxygen consumption in *L. subrostrata* as a function of dry tissue weight. The Q_{O_2} is in μl O_2/g dry tissue-hr. The slope of the regression line is -0.51 ± 0.02 (35).

Freshly collected animals excrete ammonia. The animals were placed in individual containers with tap water and aliquots taken for nitrogen determination. The average net flux of ammonium was 1.1 ± 0.1 μm N/g dry tissue-hr (15) over a one hr interval.

Oxygen consumption

L. subrostrata transferred from water to a respirometer flash consumes oxygen from the air. The weight specific Q_{O_2} is a logarithmic function of dry tissue weight (Fig 1). Although the weight range is narrow, the correlation ($r = -0.68$) is

TABLE II

L. subrostrata *oxygen consumption from water saturated air. Values are listed as mean ± 1 SEM. A, in laboratory tap water less than 5 days; B, in laboratory tap water 12 weeks; C, in sealed container with water saturated air for 30 days.*

Condition	N	Tissue dry weight, g	Q_{O_2}
A	20	1.38 ± 0.21	59 ± 6
B	5	1.40 ± 0.11	42 ± 6
C	10	1.52 ± 0.15	80 ± 8*

* $P < 0.05$.

TABLE III

L. subrostrata *oxygen consumption from air saturated pond water. Values are listed as mean ± 1 SEM. A, in laboratory pond water less than 5 days; B, in laboratory pond water 12 weeks.*

Condition	N	Tissue dry weight, g	Q_{O_2}
A	10	2.16 ± 0.30	287 ± 16
B	7	1.29 ± 0.06	185 ± 17*

* $P < 0.001$.

highly significant ($P < 0.001$). The aerial Q_{O_2} is not significantly changed after several months laboratory storage in tap water (Table II). Variability in Q_{O_2} was high, ranging from 18 to 150.

Oxygen consumption in water is significantly higher than aerial respiration (Table III). The Q_{O_2} from mussels stored in tap water several months was significantly (36%) less than recently collected animals, however, the difference in weight tends to minimize the reduction. Aquatic respiration exceeds aerial Q_{O_2} even after prolonged storage in tap water. Part of the elevated Q_{O_2} in water is due to activity; siphoning water, valve and foot movement. There was no change in Q_{O_2} when the stored animals were pretreated 24 hr with penicillin (800 u/ml) in the water: Q_{O_2} 160 ± 37 (5).

The weight specific aquatic Q_{O_2} is a logarithmic function of dry tissue weight (Fig. 2). The slope of the regression line is significantly different from that noted for aerial respiration ($P < 0.001$). All animals used for the regression analysis

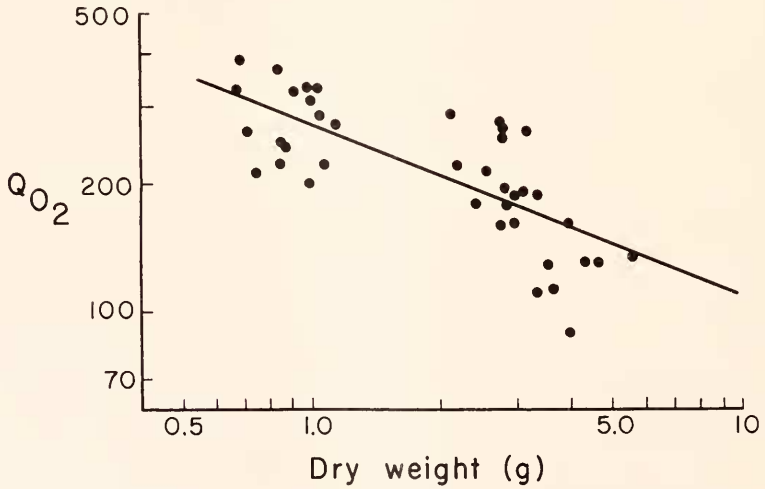

FIGURE 2. Aquatic oxygen consumption in *L. subrostrata* as a function of dry tissue weight. The Q_{O_2} is in μl O_2/g dry tissue-hr. The slope of the regression line is -0.40 ± 0.06 (39) and the correlation is highly significant ($r = -0.75$, $P > 0.001$).

were stored in pond water less 7 days. By 14 days a detectable drop of Q_{O_2} was noted which becomes pronounced with long term storage (*cf.* Table III).

Effects of prolonged exposure to air

Animals transferred to a sealed container, with water saturated air and CO_2 absorbant, moved intermittently during the first few hours. After 12 hr, movement ceased and the valves appeared closed. The animals continued to consume O_2 from the atmosphere even after 30 days exposure. The Q_{O_2} was higher than values observed for animals out of water less than 3 hr, however, part of the increase may be due to microbe contamination, which was not controlled. These animals lost 1.44 ± 0.16 g/10 g fresh tissue weight over the 30 day interval. However, the body fluid composition was similar to that found in animals subjected to 2 days dehydration at lower humidity (see below).

Total tissue glycogen in freshly collected mussels was 0.36 ± 0.02 g/g dry tissue (10). Tissue carbohydrate was unchanged after the animals were exposed to air (high humidity) for 40 days (36 ± 1% of dry weight, N = 10). This is 88–95% of tissue glycogen from fresh animals at that season.

Survival of *L. subrostrata* is reduced to 6–10 days if they are exposed to a low relative humidity atmosphere (45–55%) at 25° C. Oxygen consumption from air is significantly increased after 4–5 days dehydration: Q_{O_2} 100 ± 24 (7). Microbial contamination may contribute to the elevated Q_{O_2}. Particulate matter accumulates in the mantle cavity near the siphons when dehydrated. These animals lost 2.40 ± 0.68 g/10 g fresh tissue weight.

During dehydration, the rate of evaporative water loss is relatively constant over a 4 day period (30 µl/10 g fresh tissue-hr). The loss of water results in an increased body fluid total solute concentration (Table IV). The highest total solute measured was 160 mOsmoles/l. The initial changes in calcium are higher than expected and may be due to calcium dissolved from the shell to buffer accumulation of metabolic products. Both lactate and NPS are elevated relative to

TABLE IV

Effect of dehydration on body fluid ion composition in L. subrostrata. *Data are expressed as mean ± 1 SEM, number of animals in parenthesis. Animals were maintained in air at 25° C, 45 to 55% relative humidity.*

Component	Units	Days of dehydration		
		2	4	7
Total solute	mOsm/l	68.8 ± 1.7 (8)	89.0 ± 2.7 (12)	91.9 ± 7.8 (14)
Na	mM/l	24.5 ± 0.8 (8)	32.9 ± 0.6 (12)	37.5 ± 1.2 (14)
Cl	mM/l	18.4 ± 0.6 (8)	29.4 ± 1.7 (12)	35.2 ± 2.0 (14)
Ca	mM/l	8.4 ± 0.6 (8)	8.0 ± 0.9 (9)	—
Lactate	mM/l	0.3 ± 0.1 (8)	0.8 ± 0.2 (7)	0.8 ± 0.2 (7)
NPS	mM/l	3.6 ± 0.1 (8)	2.8 ± 0.2 (12)	3.8 ± 0.5 (7)
Total H_2O loss	g/10g*	1.46 ± 0.22 (8)	2.85 ± 0.03 (8)	3.44 ± 0.14 (7)

* Based on initial fresh tissue weight.

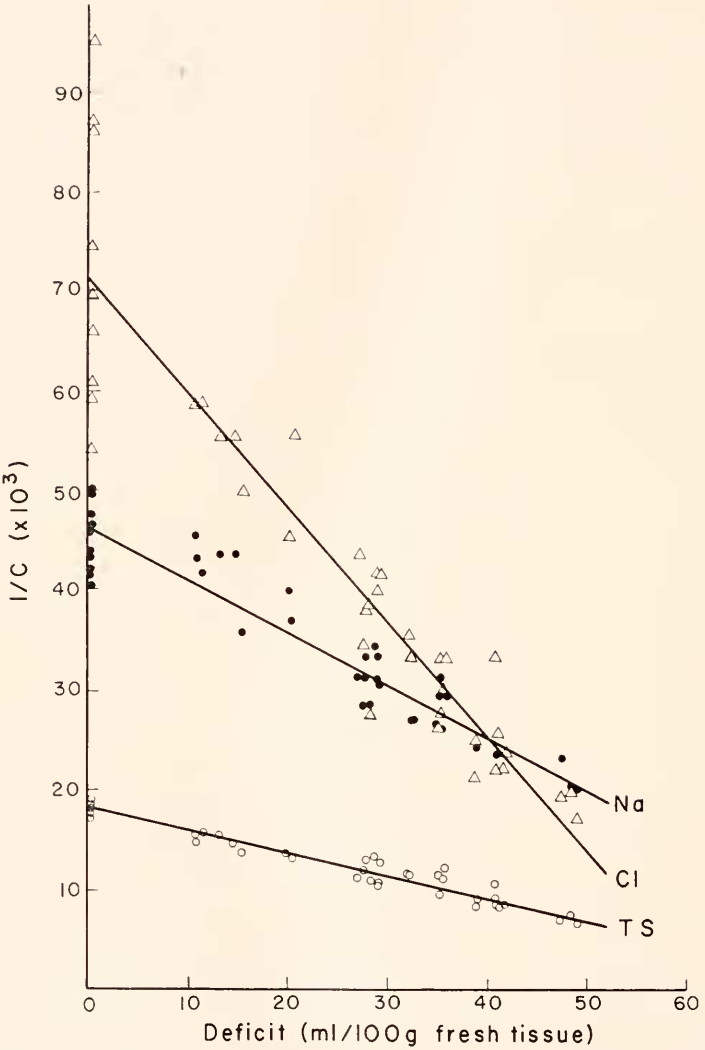

FIGURE 3. The effect of dehydration on solute concentration in the body fluids of *L. subrostrata*. The abscissa is the water lost during dehydration. The deficit is based on initial fresh tissue weight excluding the shell and mantle cavity water. The ordinate is the reciprocal of solute concentration $(\text{mM}/1)^{-1}$ multiplied by 10^3. TS is the total solute $(\text{mOsm}/1)^{-1}$. Number of animals used for determining the regression lines was 46.

tap water controls. However, no major changes were noted with prolonged dehydration.

It is possible to relate the body fluid solute concentration to the degree of dehydration in an animal (Alvarado, 1972). Assuming the water in a compartment is available as solvent and, if there are no changes in the solute content in the com-

partment, then it is possible to predict the body fluid concentration as a function of water deficit:

$$C = (C_o \cdot V_o)/(V_o - D) \quad (1)$$

Where C_o and V_o are the solute concentration in the body fluids and total water content of a hydrated animal (excluding the shell), respectively; C is the body fluid solute concentration after dehydration and D is the water deficit. The reciprocal of Equation 1 can be rearranged into an equation for a straight line:

$$1/C = 1/C_o - D/(C_o \cdot V_o) \quad (2)$$

Figure 3 shows the data plotted using Equation 2. The correlation between water deficit and Cl, Na or total solute is highly significant ($P < 0.001$) with correlation coefficients (r) for each regression line: −0.90, −0.95 and −0.97, respectively. Linear regression estimates of the Y-intercept ($1/C_o$) and the X-intercept (V_o) are presented in Table V. The calculated and observed C_o values are in agreement. However, the V_o estimates from Cl and total solute are significantly different from the observed values. These data indicate a shift of Cl out of tissues into the body fluid.

Effects of anoxia

Exposure of *L. subrostrata* to water saturated N_2 atmosphere resulted in a significant behavioral change. Within 12 hr of exposure to anoxic conditions, the valves gaped and the foot was extended several centimeters. This is apparently an attempt to expose additional tissue surface area for oxygen absorption. Living animals responded to repeated mechanical stimulation by slowly withdrawing the foot but re-extend it within a few hr. These animals could survive 4–6 days anoxia. The magnitude of oxygen debt was noted when 7 animals were returned to air in a respirometer flask: Q_{O_2} 249 ± 56 over a 1 hr interval. Total tissue glycogen was not changed from the tap water acclimated animals.

Exposure of *L. subrostrata* to a N_2 atmosphere resulted in significant changes in the body fluid composition (Table VI). Total solute increased rapidly even though dehydration was minimized. The maximum total solute measured in a

TABLE V

Calculated and observed values of solute concentration and water content of L. subrostrata. *All values are mean ± 1 SEM, number of animals in parentheses.*

Solute	C_o(mM/l)		V_o(ml/100 g tissue)	
	Calculated*	Observed	Calculated*	Observed
Na	21.7	21.0 ± 0.6 (26)	89.1	87.7 ± 0.4 (18)
Cl	14.0	12.0 ± 0.6 (26)	62.6**	87.7 ± 0.4 (18)
Total solute	54.4	53.0 ± 0.6 (26)	79.9**	87.7 ± 0.4 (18)

* From least squares regression estimates, n = 46.
** $P < 0.001$.

TABLE VI

Effect of N_2 atmosphere on body fluid ion composition in L. subrostrata. *Data are presented as mean ± 1 SEM, number of animals in parentheses. Animals were in sealed containers at 25° C, 100% R.H. gassed with N_2 twice daily.*

Component	Units	Days of anoxia	
		2	4
Total solute	mOsm/l	107 ± 7 (14)	121 ± 6 (20)
Na	mM/l	20.0 ± 0.6 (14)	19.9 ± 0.6 (20)
Cl	mM/l	12.9 ± 0.5 (14)	11.4 ± 0.6 (20)
Ca	mM/l	26.3 ± 4.0 (14)	28.0 ± 3.4 (6)
Lactate	mM/l	6.3 ± 0.9 (14)	6.7 ± 1.4 (10)
NPS	mM/l	4.1 ± 0.4 (8)	4.2 ± 0.4 (4)
Weight loss	g/10g*	0.65 ± 0.15 (8)	0.69 ± 0.17 (10)

* Based on initial total animal weight.

surviving animal was 180 mOsmoles. Sodium and chloride do not change relative to tap water controls. The major ionic change is a 5 to 8 fold increase in calcium and the unidentified anion (see discussion). The highest measured calcium concentration was 41 mM/l. The body fluid lactate concentration also increased 50 fold relative to tap water animals but the contribution to total solute is small. The NPS increased above tap water animals but the chemical nature is not known. The weight loss may be due to dissolved shell and subsequent evolution of CO_2 rather than water loss since the Na and Cl concentrations were not changed.

Although few animals survive longer than 4–6 days in a N_2 atmosphere, survival is extended if the animals are immersed in N_2 gassed water (> 15 days). The animals did not extend the foot but all siphoned water. Apparently these animals do not accumulate an oxygen debt under these conditions. When returned to air the Q_{O_2} was 73.0 ± 14.6 (5) over a 1 hr interval.

The body fluid composition is modified when exposed to N_2 gassed pond water (Table VII). The body fluid total solute is significantly higher than animals in aerated tap water but less than animals in N_2 atmosphere. Calcium and lactate

TABLE VII

Effect of exposure to N_2 gassed water on body fluid ion composition in L. subrostrata. *Data are presented as mean ± 1 SEM.*

Component	Units	Days exposure*	
		4	15
Total solute	mOsm/l	63 ± 2	68 ± 1
Na	mM/l	15.4 ± 0.5	12.4 ± 0.4
Cl	mM/l	6.0 ± 0.3	4.1 ± 0.2
Ca	mM/l	14.4 ± 1.0	10.9 ± 0.6
Lactate	mM/l	0.26 ± 0.05	0.23 ± 0.03

* N = 6 animals for each experiment.

are elevated in response to anoxia but excess metabolic acids are apparently excreted. The measured net loss of calcium to the bathing medium was 2.0 ± 0.1 μm Ca/10g fresh tissue-hr over 15 days exposure to N_2 gassed water. Metabolic acid excretion was not monitored because of potential decomposition by microbes in the water. The reduction in body fluid sodium and chloride is significant but has not been pursued.

Discussion

If water loss is retarded, *L. subrostrata* will survive over 40 days in air and other pelecypods exceed three weeks (Bayne, 1973; Dugal, 1939). Dance (1958) has reported a freshwater mussel survived 12 months out of water. Those animals which have been studied were not anoxic but consumed O_2 from the atmosphere (Coleman, 1973; Kuenzler, 1961; Lent, 1968). The limiting factor for survival in air is primarily tolerance to desiccation. Although the body fluids of freshwater mussels are dilute (Potts, 1954), *L. subrostrata* will tolerate a three fold increase in body fluid total solute, with an upper limit of 160 mOsmoles. Analyses of the body fluids indicate the higher osmolarity is due to water loss and concentration of solutes rather than a build up of metabolic products.

It is noteworthy that these animals tolerate extensive changes in body fluid total solute and qualitative changes in ionic composition. They are able to survive a large increase in NaCl concentration during dehydration and an 8 fold increase in body fluid Ca during anoxia. The shift of Cl from the tissues to the body fluid during dehydration and the reduction of body fluid Na and Cl during anoxia in water are significant but the mechanism remains obscure. Apparently, the osmolarity of body fluids is the primary factor limiting survival and the specific solutes are less important.

A source of energy for survival out of water is glycogen (Stokes and Awapara 1968; De Zwaan and Zandee, 1972b). The quantity of total carbohydrate (36% of dry tissue weight) in *L. subrostrata* is similar to other pelecypods (Badman and Chin, 1973; De Zwaan and Zandee, 1972a, 1972b). Potential survival time, in air, for an animal of one gram dry tissue weight, using glycogen only, is about 200 days. Aerobic metabolism will also allow protein and lipid catabolism. Curiously, others have noted more rapid tissue glycogen loss (Badman and Chin, 1973; De Zwaan and Zandee, 1972b). In water, *L. subrostrata* excretes ammonia but out of water the nitrogen from protein catabolism may shift into less toxic urea production (Andrews and Reid, 1972). This may contribute to the elevated NPS production noted during dehydration.

When pelecypods are returned to water, oxygen consumption is higher with a Q_{O_2} about 3–4 times the aerial rate (Coleman, 1973; Kuenzler, 1961; Moon and Pritchard, 1970). This is probably reflecting the increased energy required in moving water to irrigate the mantle cavity. Animals recently collected have a greater Q_{O_2} in water than animals stored in the laboratory for a period of time. Which value is "normal" cannot be established by these experiments. The higher Q_{O_2} may be due to greater foot movements, especially prominent during the first 2 weeks, or ventilation "searching" for food. Animals under both conditions have a high glycogen content so depletion of food stores is not the primary reason for

low Q_{O_2} in laboratory adapted *L. subrostrata*. However, it has been suggested that starvation is the reason for the lower Q_{O_2} in some gastropods which have a lower carbohydrate reserve (von Brand, Baerstein and Mehlman, 1950). A transient higher Q_{O_2} immediately after reimmersion in water (Moon and Pritchard, 1970) may be due to some oxygen debt or the energy required to remove trapped air and wastes accumulated in the mantle cavity during exposure to air (Boyden, 1972). Specimens of *L. subrostrata* were observed to open the valves allowing air to escape from ventral and posterior shell margins followed by forceful adduction of the shell which expelled additional air and particulate matter from the siphon area.

L. subrostrata is a facultative anaerobe. However, when exposed to anoxic conditions out of water, survival time is not longer than animals exposed to dehydration in air (5–7 days). The body fluid total solute is elevated after prolonged exposure to N_2 but the maximum concentration tolerated is 180 mOsm. This is about the same for animals exposed to dehydration. However, the principal solutes contributing to the osmolarity in anoxic animals are calcium and its anion; probably bicarbonate and succinate (Dugal, 1939; Potts, 1954; Stokes and Awapara, 1968; De Zwaan and Zandee, 1972a, 1972b).

The ability of *L. subrostrata* to tolerate prolonged anoxia in water (>15 days) is of ecologic significance. It is not unusual for water with a high organic content to drop to near zero oxygen for extended periods. Some gastropods will also tolerate anoxia in excess of two days, although there are considerable species differences (von Brand, *et al.*, 1950).

The metabolic adaptations to facultative anaerobiosis in bivalves include production of the less toxic alanine and the less soluble succinate salts rather than lactate (Stokes and Awapara, 1968; De Zwaan and Zandee, 1972b). Recently, Hochachka and Mustafa (1973) have demonstrated that anaerobic metabolism in the Pacific oyster is adapted to generate additional substrate level phosphorylation as α-ketoglutarate is shunted into the Krebs cycle (Mustafa and Hochachka, 1973). The ability to excrete metabolic acids to the environment is energetically expensive but prevents the build up of body fluid osmolarity which would be lethal.

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Summary

1. *Ligumia subrostrata,* removed from water will survive >40 days if dehydration is minimized by high relative humidity. They are not anoxic but consume oxygen from the air (Q_{O_2} 59 μl O_2/g dry tissue-hr). One source of energy is from the large glycogen stores (36% of dry tissue).

2. Animals removed from water and exposed to either low relative humidity (45–55%) or N_2 atmosphere will survive about 5–7 days. The maximum total solute in the body fluids of surviving animals is 160–180 mOsmoles.

3. Sodium, Cl, K, and Ca account for 72% of the total solute in the body fluids of fresh water acclimated animals. Dehydration increases the concentration of Na proportional to the amount of water lost. There is a significant shift of Cl from the tissues into the body fluids during dehydration.

4. When the animals are out of water, forced anoxia increases the body fluid total solute but the Na and Cl contribution is small. The major ions in the body fluids are calcium and bicarbonate or succinate; reflecting a build up of metabolic acids. Lactate concentration in the body fluids is low. These animals experience a significant oxygen debt since oxygen consumption is elevated when returned to air (Q_{O_2} 249 μl O_2/g dry tissue-hr).

5. Mussels are facultative anaerobes and will survive for extended periods of time in N_2 gassed water (< 54 μl O_2/l). The body fluids are slightly changed from normal suggesting the metabolic products are excreted. These animals do not suffer an oxygen debt.

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